

Genera of the parasitoid wasp family Monomachidae (Hymenoptera: Diaprioidea)

NORMAN F. JOHNSON^a & LUCIANA MUSETTI^b

^aDepartment of Evolution, Ecology & Organismal Biology, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212, USA; e-mail: johnson.2@osu.edu;

urn:lsid:zoobank.org:author:3508C4FF-F027-445F-8417-90AB4AB8FE0D

^bDepartment of Evolution, Ecology & Organismal Biology, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212, USA; e-mail: musetti.2@osu.edu;

urn:lsid:zoobank.org:author:107E9894-C9AB-4A8B-937E-5007703FD891

urn:lsid:zoobank.org:pub:64843E54-8936-4956-B1FD-2381214CE77A

Abstract

The genera of the family Monomachidae are revised. *Chasca* Johnson & Musetti, **new genus**, is described, with two species: *Chasca andina* Musetti & Johnson, **new species** (type species, Chile) and *C. gravis* Musetti & Johnson, **new species** (Peru). The genus *Tetraconus* Szépligeti is treated as a junior synonym of *Monomachus* Klug (**new synonymy**), and its type species is transferred to *Monomachus* as *M. mocsaryi* (Szépligeti), **new combination**. A phylogenetic analysis places *Chasca* and *Monomachus* as sister-groups; within *Monomachus*, the three species of Australia and two species of New Guinea are basal, and the radiation of 21 species in tropical America and Valdivia is recovered as a monophyletic group.

Key words: Hymenoptera, key, phylogeny, parasitoid

Introduction

The family Monomachidae (Hymenoptera: Diaprioidea) is a small group of parasitoid wasps with two recognized genera: *Monomachus* Klug and *Tetraconus* Szépligeti (Naumann 1985, Musetti & Johnson 2004). Adults are generally small to medium-sized, and females are readily recognized by their elongate, loosely articulated, weakly sclerotized, and acuminate metasoma. Males are more generalized in appearance, with an elongate petiole and clavate gaster (metasoma beyond the petiole), and have the general appearance of small ichneumonoids. The autapomorphic structure of the female metasoma and the strongly reduced ovipositor suggest that the family is monophyletic. Monomachidae traditionally has been relegated to the superfamily Proctotrupoidea (e.g., Naumann & Masner 1985), but Rasnitsyn (1980) and, more recently, Sharkey (2007) have placed them in a separate superfamily of the infraorder Proctrupomorpha, the Diaprioidea, together with the New Zealand endemic Maamingidae and the cosmopolitan and speciose Diapriidae. This relationship was suggested by Dowton & Austin (2001), Castro & Dowton (2006), Heraty *et al.* (2011) and Sharkey *et al.* (2011), but was not supported by the analysis of Vilhelmsen *et al.* (2010). Sharkey *et al.* (2011) also included the family Ismaridae within Diaprioidea; in other studies this taxon was considered a subfamily of Diapriidae.

Little is known of the biology of monomachids. Naumann (1985, 1991) reported that one Australian species, *Monomachus antipodalis* Westwood, is an egg-larval or egg-pupal parasitoid of species of the soldier fly genus *Boreoides* (Diptera: Stratiomyiidae: Chiromyzinae). The Neotropical species *M. fuscator* Perty and *M. eurycephalus* Schletterer have been reared from the coffee pest *Chiromyza vittata* Wiedemann (also Chiromyzinae) (Musetti & Johnson 2004). Males predominate in collections: Musetti & Johnson (2004) reported that only 17.2% of specimens in collections are females, suggesting that the two sexes occupy different habitats as adults.

Tetraconus is known only from a single female specimen collected in the Brazilian state of Espírito Santo at the end of the 19th Century (Szépligeti 1903). *Monomachus* has a transantarctic distribution: three species—*M. antipodalis* Westwood, *M. australicus* Girault, and *M. hesperius* Naumann—are known from Australia (Naumann 1985); two species—*M. cracens* Musetti & Johnson and *M. comptus* Musetti & Johnson – have been recorded from New Guinea (Musetti & Johnson 2000); and twenty one species are known from the tropics of North, Central and South America as well as Valdivia (Musetti & Johnson 2004).

The existence of species with micropterous females from Peru and Chile was reported by Naumann (1985) and Masner (1993). Naumann suggested that these species may warrant recognition as a new genus, and Naumann & Masner (1985) asserted in their key to families of proctotrupoids that there are three genera of monomachids. The goal of this work was to examine the generic concepts within the framework of a phylogenetic analysis of the species of the family, specifically to address the monophyly of *Monomachus* and the status of *Tetraconus* and the micropterous species.

Materials and Methods

The sources of specimens of Neotropical and New Guinea *Monomachus* for this study are listed in Musetti & Johnson (2000, 2004). Additional specimens for this work are deposited in the following collections: American Entomological Institute, Gainesville, FL (AEIC)¹; Australian National Insect Collection, Canberra (ANIC)²; Canadian National Collection of Insects, Ottawa, ON (CNCI)³; Hungarian Natural History Museum, Budapest (HNHM)⁴; Museum of Comparative Zoology, Cambridge, MA (MCZC)⁵; C.A. Triplehorn Insect Collection, Columbus, OH (OSUC)⁶.

Morphological terminology follows that used in Musetti & Johnson (2000, 2004). The body length of specimens was measured in lateral view by adding the length from the anteriormost point on the head capsule to the base of the petiole and the length of a straight line from the base of the petiole to the apex of the metasoma. These values should be taken as approximate. Individuals have the body segments loosely articulated, and specimens commonly end up in fairly contorted positions when dried and mounted.

In the Material Examined the numbers prefixed with “OSUC” are unique identifiers for the individual specimens. The label data for all specimens have been georeferenced and recorded in the Hymenoptera On-Line database⁷, and details on the data associated with these specimens can be accessed at the following link, purl.oclc.org/NET/hymenoptera/ol, and entering the identifier in the form. Note the space between the acronym and the number.

Data associated with the genus *Chasca* (described below) can be accessed at <http://hol.osu.edu/index.html?id=276540>. Species descriptions were generated using a database application, vSysLab⁸, designed to facilitate the production of a taxon by character data matrix, and to integrate those data with the existing taxonomic and specimen-level database. Data may be exported in both text format and as input files for other applications. The text output for descriptions is in the format of “Character: Character state(s).” Images and measurements were made using AutoMontage and Cartograph extended-focus software, using JVC KY-F75U digital camera, Leica Z16 APOA microscope, and 1X objective lens. Images are archived at Morphbank and in Specimage⁹, the image database at The Ohio State University.

-
1. <http://biocol.org/urn:lsid:biocol.org:col:1008>
 2. <http://biocol.org/urn:lsid:biocol.org:col:32981>
 3. <http://biocol.org/urn:lsid:biocol.org:col:1012>
 4. <http://biocol.org/urn:lsid:biocol.org:col:33453>
 5. <http://biocol.org/urn:lsid:biocol.org:col:33791>
 6. <http://biocol.org/urn:lsid:biocol.org:col:1014>
 7. <http://hol.osu.edu>
 8. <http://vsyslab.osu.edu>
 9. <http://specimage.osu.edu>

In this article we have followed the precedent of Pyle et al. (2008) and Johnson et al. (2008) in the implementation of biodiversity informatics standards within a taxonomic publication. The electronic version of the paper contains hyperlinks to external resources. Insofar as possible the external information conforms to standards developed and maintained through the organization Biodiversity Information Standards (Taxonomic Database Working Group). All new species have been prospectively registered with Zoobank (Polaszek et al. 2005), and other taxonomic names, where appropriate, have been retrospectively registered. The external hyperlinks are explicitly cited in the footnotes so that users of the printed version of this article have access to the same resources. Life sciences identifiers, LSIDs, may be resolved at the specified URLs or at lsid.tdwg.org.

All known species of Monomachidae were included in the phylogenetic analysis. Outgroups included in the matrix were *Ropronia garmani* Ashmead (Roproniidae), *Maaminga rangi* Early et al. (Maamingidae), *Dissoxylobis* sp. (Diapriidae), and *Ismarus* sp. (Ismaridae). Characters and character states are listed in the appendix. Since the focus of the analysis was relationships within Monomachidae, few characters were included the support the monophyly of the family. All characters were treated as nonadditive. Maximum parsimony and implied weighting analyses were conducted using TNT version 1.1 (Goloboff et al. 2000); the implied weighting used the default K value (k=3) and the command xmult. Branch support was estimated by implied weighting analysis of 1000 bootstrapped samples.

Results and Discussion

Maximum parsimony analyses resulted in 84 equally parsimonious trees (not illustrated). Implied weighting resulted in only three trees (Fig. 1), differing only in the relationships of *M. klugi*, *M. megacephalus* and *M. satyrus*+*Tetraconus mocsaryi*. Monomachidae is recovered as a monophyletic unit. Within that, the two micropterous species (formally described below as *Chasca*) are recovered as a monophyletic unit, followed by a monophyletic group comprising all species of *Monomachus* and *Tetraconus*. The three species from Australia and the two species from New Guinea are basal within this *Monomachus* clade. The sole species of *Tetraconus*, *T. mocsaryi*, is placed as the sister group of *M. satyrus* Musetti & Johnson deep within the clade of New World *Monomachus*. *Tetraconus* shares the rich brown body color and infusate tips of the fore wings found in *M. satyrus*, *M. megacephalus* and similar large species. The peculiar clypeal tubercles to which Naumann (1985) referred in his key to monomachid genera are also found in *M. satyrus*.

Continued recognition of *Tetraconus* as a distinct genus is inconsistent with retaining the monophyly of *Monomachus*. Therefore, we propose that *Tetraconus* be considered to be a junior synonym of *Monomachus*, **new synonymy**, and *T. mocsaryi* is transferred to that genus as *Monomachus mocsaryi*, **new combination**. Townes (1977) and Naumann (1985) earlier suggested that *Tetraconus* may be untenable, but neither formally proposed it as a synonym. The sole specimen of *T. mocsaryi* is unusually large for the genus (fore wing length = 9.8 mm), and its bizarre genal tubercles (Figs. 2, 3) may be an allometric consequence of its size.

Inclusion of *M. mocsaryi* within *Monomachus* necessitates a minor emendation to the key to species of the New World (Musetti & Johnson 2004) by inserting the following couplet between the existing couplets 1 and 2:

- | | | |
|------|---|---|
| 1.5. | Lower gena produced posteriorly into elongate, rounded tubercles (Figs. 2, 3) | <i>M. mocsaryi</i> (Szépligeti), n.comb. |
| – | Lower gena broadly rounded posteriorly, tubercles absent | 2 |

The two micropterous species consistently emerge as basal to all other species of monomachids. Only a single character is indicated as a synapomorphy in Fig. 1, the reduction of wings in the female, but this is because we chose to illustrate only non-homoplasious characters for the purposes of clarity. The two species also share another apomorphy, the open radial cell in the fore wing of the male. This character is also found in *M. paulus* Musetti & Johnson, a species from Argentina. However, this is very likely a convergence, as *M. paulus* has all the characters of the mandible and clypeal margin that place it within the clade of Neotropic *Monomachus*.

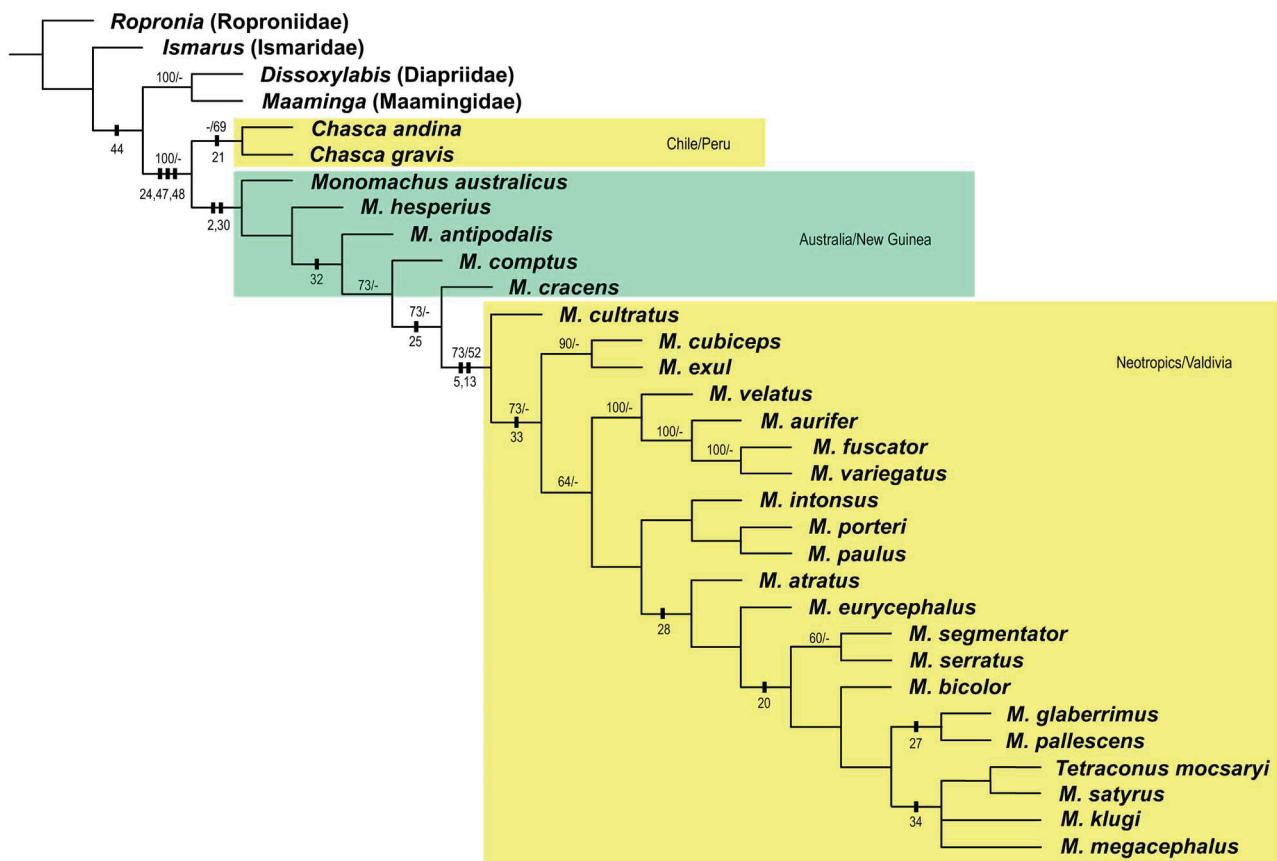
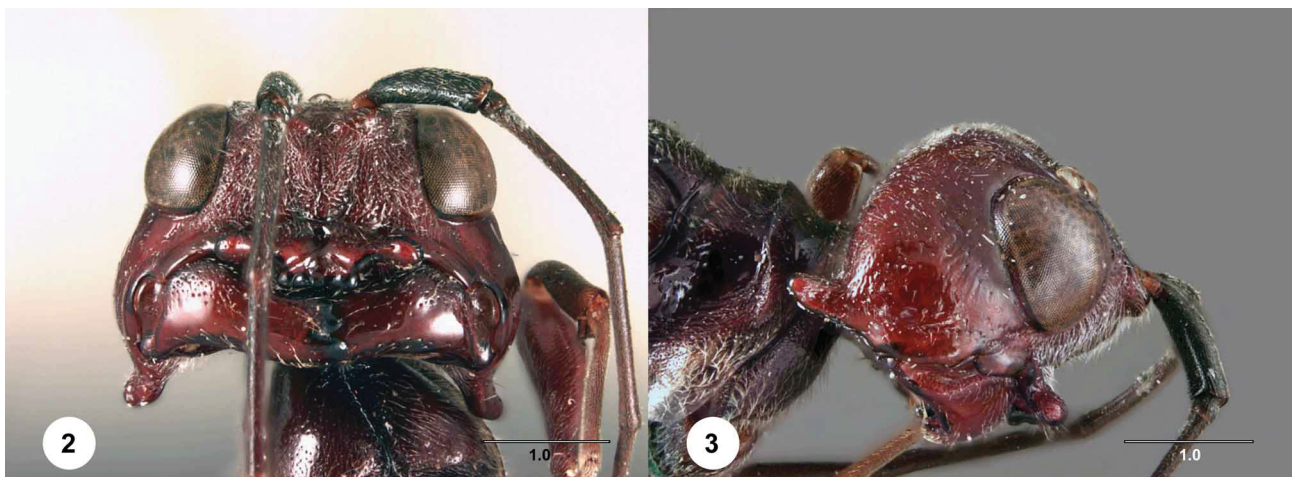


FIGURE 1. Relationships within the family Monomachidae, derived from implied weighting analysis implemented in TNT (Goloboff *et al.* 2003). Only non-homoplasious characters are mapped on the cladogram. Numbers below the branch refer to characters. Numbers above are the percentage of trees recovered in maximum parsimony analyses containing the subtended clade, followed by the bootstrap values for 1000 replications and analyzed with implied weighting. Values <50% not shown.



FIGURES 2–3. *Monomachus mocsaryi* (Szépligeti), holotype female. **2**, head, frontal view; **3**, head, lateral view. Scale bars in mm. Morphbank: <http://www.morphbank.net/?id=579905>

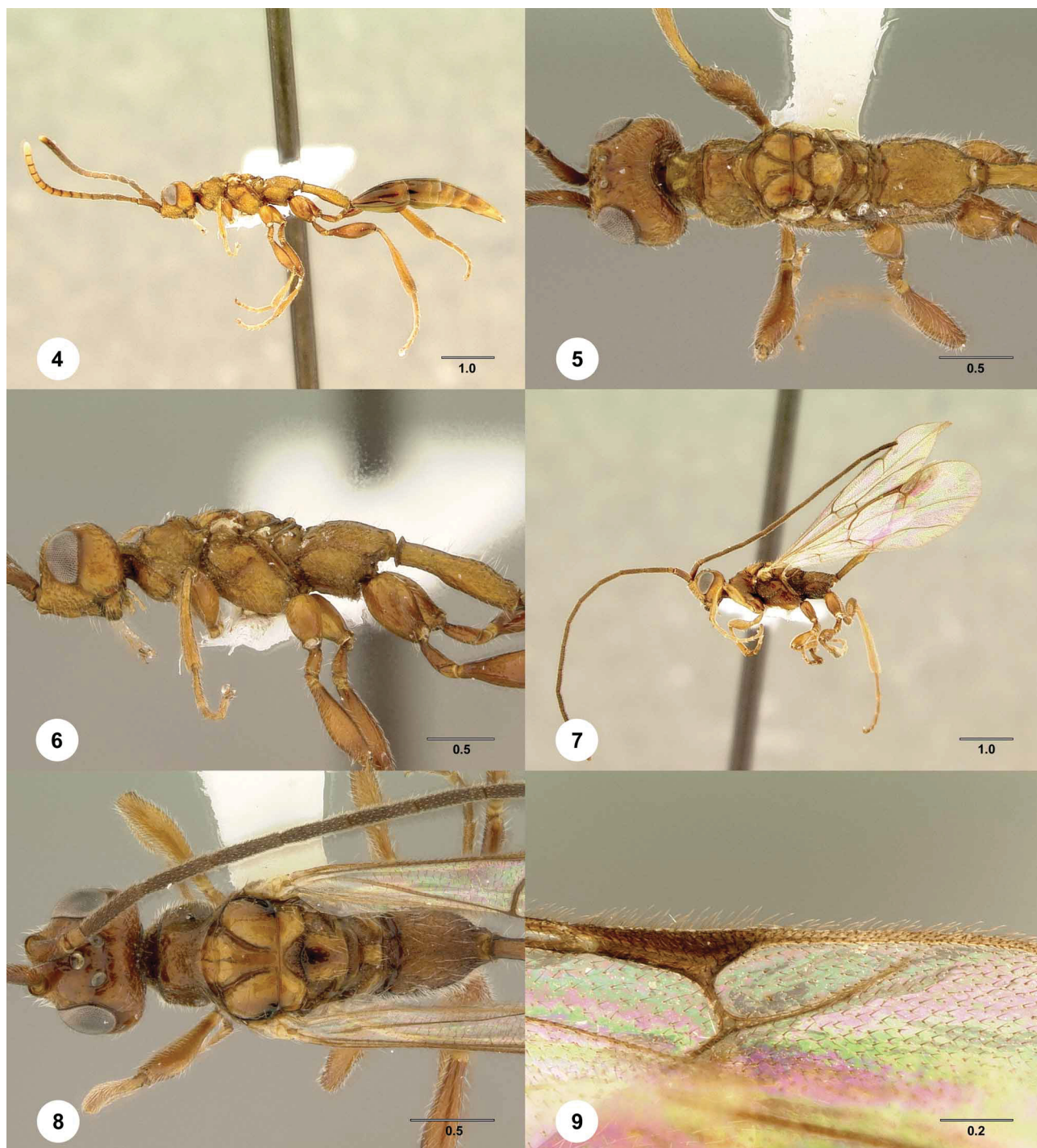
***Chasca* Johnson & Musetti, new genus**

urn:lsid:zoobank.org:act:0DD25D3C-48C2-40BC-A599-2DC850EE0AB7

urn:lsid:biosci.ohio-state.edu:osuc_concepts:276540

Figures 4–15

Type species: *Chasca andina* Johnson & Musetti, n.sp.



FIGURES 4–9. *Chasca andina* Musetti & Johnson. **4**, lateral habitus, holotype female (OSUC 186320; **5**, head and mesosoma, dorsal view, holotype female; **6**, head and mesosoma, lateral view, holotype female; **7**, lateral habitus, paratype male (OSUC 18633); **8**, head and mesosoma, dorsal view, paratype male (OSUC 18633); **9**, stigma and radial cell of fore wing, paratype male (OSUC 18633). Scale bars in mm. Morphbank: <http://www.morphbank.net/?id=579899>

Description. Female. Length: 6.6–8.7 mm. **Head** in frontal view quadrate; head width across gena subequal to width across compound eyes; frons moderately convex; antennal insertions raised, forming modest raised ledge between eyes, divided medially by depressed area; inner margins of eyes weakly diverging ventrally; malar area posterior to malar sulcus mostly smooth, with few setigerous punctures, anterior to sulcus punctate; malar sulcus well-defined; apical margin of clypeus without teeth or lobes, longest medially; ocelli in small medial triangle, OOL > POL; vertex sculpture variable; occipital carina complete, reaching hypostomal carina ventrally; hypos-

toma narrow, weakly sclerotized; antenna flagelliform, 15-merous, inserted far above clypeus; flagellomeres covered with short bristles, longer fine hairs sparsely distributed; A2 short, length approximately 2 times width, A3–15 elongate, uniform in width; mandible relatively narrow, longer than wide, bidentate apically, teeth broadly acute; distignath weakly convex, not swollen basally; basal margin of distignath not expanded; basignath small, broadly fusiform.

Mesosoma: pronotal sculpture variable, produced anteriorly into distinct neck, transition between neck and collar marked by transverse carina; mesoscutum smooth, sparsely setose; notaulus present, arcuate, smooth; parapsidal furrow present; axilla smooth, sparsely setose, separated from disc of mesoscutellum by crenate furrow; mesoscutellar pit variable in shape, not crenulate anteriorly; central disk of scutellum quadrate, slightly longer than wide, posterior margin with single transverse row of subapical punctures; mesoscutellum largely smooth, with few scattered punctures; metascutellum (dorsellum) bulging, subquadrate; metapostnotum with pair of rounded posterior projections; mesopleuron punctate anteriorly, setose anteriorly and ventrally, with wide, smooth, nearly glabrous area adjacent to mesopleural sulcus; mesepisternal groove indicated by foveate line; scrobal groove indicated by transverse foveate line; mespisternum finely punctate, setose, protuberant ventrally; discrimen indicated by deep foveate longitudinal line of inflection, widened posteriorly to form small fusiform pit anterior to mid coxae, margin of pit strongly produced into fingerlike projections; metapleuron distinctly separated from propodeum by line of foveae, densely setose, coarsely sculptured; propodeum elongate, bulging dorsally, coarsely sculptured, setose throughout, with weak median longitudinal carina in anterior half; anterior margin of propodeum with pair of teeth opposite metapostnotal projections; fore and hind wings strongly reduced, brachypterous or micropterous; tibial spur formula 1-2-2; hind tibia without distinct scar at position of subgenual organ, distinctly, though weakly expanded in distal two-thirds; all tarsi 5-segmented, basitarsus longest tarsomere on all legs; pretarsal claws simple.

Metasoma: petiole moderately long (in comparison with many species of *Monomachus*), robust, weakly to moderately bowed; segment 2 subequal in length to segment 3, only slightly widened apically; segments 2–5 as wide as high, not strongly compressed laterally; terga, sterna strongly sclerotized, loosely connected, lateral margins of terga surrounding sterna; ovipositor apparently minute, not visible externally; cercus platelike.

Male. Very similar to typical *Monomachus*; length of body 5.0–7.5 mm; fore wing length 3.9–5.8 mm; antenna 14-merous; fore wing with radial cell open apically (Fig. 9); base of m-cu strongly displaced basad of bifurcation of Cu_{1b}; cercus digitiform.

Etymology. The generic name refers to Chasca, the Incan goddess of dawn and dusk. The grammatical gender of the name should be considered as feminine.

Diagnosis. Females of *Chasca* are immediately distinguishable from all *Monomachus* by their shortened wings. Males are separable from most *Monomachus* by the open radial cell in the fore wing. This character is shared with *M. paulus*, a species from Argentina. *Chasca* may be distinguished from this species by the rounded to sinuate ventral margin of the clypeus that lacks the small submedial teeth of *M. paulus*; the subequal, rounded to acute pair of mandibular teeth; and the small fusiform basignath. These differences may be summarized as follows:

Key to genera of Monomachidae

1. Female brachypterous or micropterous (Figs. 4, 10); male with radial cell of fore wing open apically (Figs. 7, 9, 13); clypeus longest medially, ventral margin broadly rounded to sinuate; mandible bidentate, teeth rounded to acute, subequal in size; basignath fusiform; m-cu intersecting Cu basad of Cu_{1b} *Chasca*
- Female macropterous; male, with the exception of one species (*M. paulus* Musetti & Johnson), with radial cell of fore wing closed; if radial cell open, then ventral margin of clypeus with two small, submedian teeth; mandible with a large, truncate posterior tooth; basignath quadrate and m-cu intersecting Cu at Cu_{1b} *Monomachus*

Chasca andina Musetti & Johnson, new species

urn:lsid:zoobank.org:act:EF0EB399-FF7D-43CF-A451-E6471F2A229C

urn:lsid:biosci.ohio-state.edu:osuc_concepts:276541

Figures 4–9; Morphbank¹⁰

10. <http://www.morphbank.net/?id=579899>

Description. Body length of female: 6.6–8.7 mm (n=8). Body length of male: 5.0–6.8 mm (n=21). Fore wing length of male: 3.9–4.8 mm (n=17). Body color of female: head, mesosoma light brown to reddish brown, metasoma brown. Sculpture of female vertex: irregularly punctate (Fig. 5). Frontoclypeal suture of female: deeply impressed. Ventral margin of clypeus: weakly, evenly convex. Tyloid of male antenna: indicated by longer, sub-erect seta near base of antennomere. Sculpture of female pronotum: irregularly rugulose. Length of notaulus: per-current (Fig. 5). Posterior separation of notauli: closely approximated, separated by distance subequal to width of notaulus (Fig. 5). Shape of mesoscutellar pit: semicircular. Sculpture of female mesopleural depression: irregularly rugulose punctate (Fig. 6). Length of female fore wing: minute, not surpassing posterior margin of mesoscutellum (Figs. 4–6). Length of female hind wing: minute, not surpassing posterior margin of metanotum.

Diagnosis. *Chasca andina* may be distinguished in the female sex by the extremely reduced wings, the reddish color of the head and mesosoma, and the coarse sculpture of the vertex and pronotum. Males may be distinguished from *C. gravis* by the absence of raised tyloids on antennomeres 4–7.

Etymology. The epithet *andina* is an adjective referring to the Andes Mountains.

Link to Distribution Map. [<http://hol.osu.edu/map-full.html?id=276541>]

Material Examined. *Holotype*, female: **CHILE**: Bio-Bío Reg., Concepción Prov., Hualpén Commune, road to Ramuntcho (Ramuncho), 12.IV.1980, T. Cekalovic, OSUC 18632 (deposited in CNCI). *Paratypes*: **CHILE**: 6 females, 22 males, 1 unknown, OSUC 116692 (AEIC); OSUC 117657, 117659–117666 (ANIC); OSUC 18622, 18633 (CNCI); OSUC 117241–117255 (FSCA); OSUC 19232–19233 (MCZC). Other material: **CHILE**: 1 male, OSUC 117658 (ANIC).

Comments. This species is known so far only from a small region of approximately 350 km (north to south) in central Chile. It is sympatric here with the more widespread Chilean species *Monomachus porteri* Brèthes. In contrast to *C. gravis*, several females have been collected. These vary some 25% in overall size, suggesting either variation in host species, host size, or the possibility that the parasitoid may at least sometimes be gregarious. The specimen with the identifier OSUC 117658 is broken (head and mesosoma lost) and is therefore not designated as a paratype.

Chasca gravis Musetti & Johnson, new species

urn:lsid:zoobank.org:act:D9D54C0F-0E42-4CF3-9A07-3067C115B25A

urn:lsid:bioisci.ohio-state.edu:osuc_concepts:276542

Figures 10–15; Morphbank¹¹

Description. Body length of female: 7.8 mm (n=1). Body length of male: 5.6–7.5 mm (n=12). Fore wing length of male: 4.5–5.8 mm (n=12). Body color of female: dark brown throughout. Sculpture of female vertex: smooth. Frontoclypeal suture of female: weakly indicated, nearly obsolete. Ventral margin of clypeus: sinuate, longest medially. Tyloid of male antenna: forming raised keel, highest apically (Fig. 15). Sculpture of female pronotum: smooth (Fig. 11). Length of notaulus: abbreviated posteriorly, distinctly separated from transscutal articulation (Fig. 11). Posterior separation of notauli: distinctly separated by distance subequal to 3x width of notaulus. Shape of mesoscutellar pit: transversely oval. Sculpture of female mesopleural depression: smooth (Fig. 12). Length of female fore wing: short, but distinct, extending posteriorly to propodeum (Figs. 10–12). Length of female hind wing: short, but distinct, extending posteriorly to propodeum.

Diagnosis. The female of *Chasca gravis* may be distinguished by the short, but clearly developed wings extending posteriorly to the propodeum, the dark brown color of the body, and the smooth vertex and pronotum. Males may be recognized by the strongly raised, knifelike tyloids on the basal flagellomeres.

Etymology. The adjective *gravis*, meaning heavy in Latin, refers to the generally robust habitus of the female of this species.

Link to Distribution Map. [<http://hol.osu.edu/map-full.html?id=276542>]

Material Examined. *Holotype*, female: **PERU**: Cuzco, Urubamba, 7.II–9.II.1968, A. Garcia & C. Porter, OSUC 19234 (deposited in MCZC). *Paratypes*: **PERU**: 346 males, OSUC 116694 (AEIC); OSUC 117107, 19235–19477, 19479, 19486–19513, 19517–19578 (MCZC); OSUC 19478, 19480–19485, 19514–19516 (OSUC).

11. <http://www.morphbank.net/?id=579882>

Comments. This species is only recorded so far from the region around Cuzco, Peru at an elevation of more than 3000 m. Only a single female is known, but, in contrast, over 300 males have been collected. The difference is undoubtedly due to the different biological imperatives of the two sexes, the males searching widely for females, and the females searching for hosts, probably in the litter or soil.

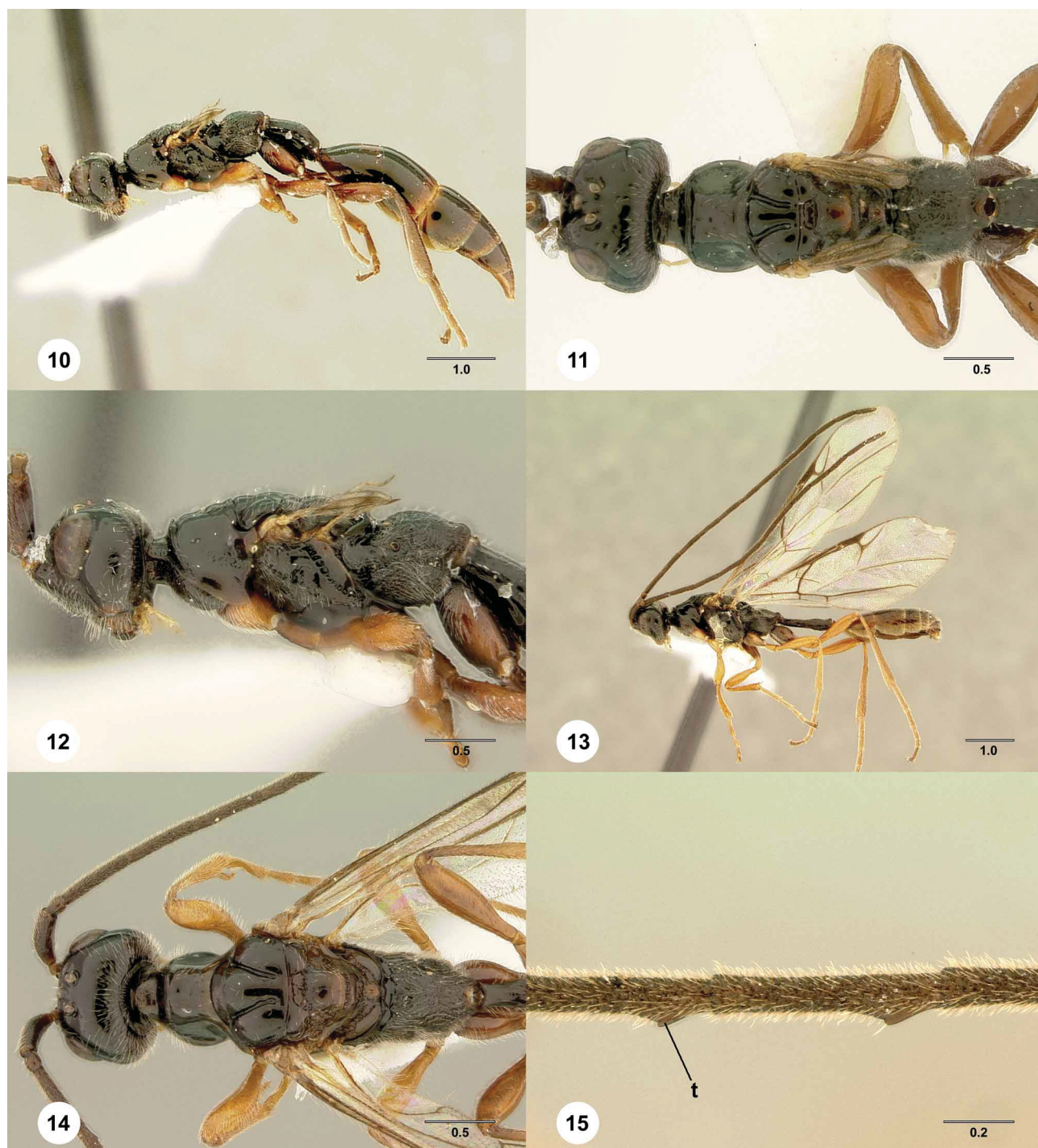


FIGURE 10–15. *Chasca gravis* Musetti & Johnson. **10**, lateral habitus, holotype female (OSUC 19234); **11**, head and mesosoma, dorsal view, holotype female; **12**, head and mesosoma, lateral view, holotype female; **13**, lateral habitus, paratype male (OSUC 19493); **14**, head and mesosoma, dorsal view, paratype male (OSUC 19574); **15**, antennomeres 4–5, paratype male (OSUC 19485). *t*, tyloid. Scale bars in mm. Morphbank: <http://www.morphbank.net/?id=579882>

Biogeography of Monomachidae. Interpretation of Fig. 1 in the context of the biogeographic history of the family must be tempered by acknowledging the weakness of the available anatomical characters for inferring phylogenetic relationships. However, *Chasca* consistently emerges as the most basal clade followed by the the Austr-

lian/New Guinea species, and these followed by the flowering of Neotropical *Monomachus*. It is tempting to interpret this as a transantarctic distribution generated by vicariance of the southern continents. However, *C. gravis* is found well north of the Atacama Desert, and *M. porteri* is widespread in Chile, both facts muddying that simple hypothesis. An alternative hypothesis, that the current biogeographic pattern represents an ancestral widespread distribution disrupted by subsequent extinction may appear less parsimonious, but should not be rejected out of hand because there are many examples of putatively “southern” taxa that also occur as inclusions in Baltic amber e.g., the proctotrupoid genus *Peradenia* (Johnson et al. 2001). The vicariance hypothesis could be strengthened by additional evidence supporting the monophyly of the Australia/New Guinea species, most likely using sequence data.

Acknowledgments

Many thanks to the curators of the collections for tolerating the protracted loans for us to study the material: D. Wahl (AEIC), J. LaSalle (ANIC), A. Bennett (CNCI), J. Wiley (FSCA), S. Csősz (HNHM), and S. Cover and P. Perkins (MCZC). A. Valerio assisted with the phylogenetic analysis; J. Cora with databasing issues; S. Hemly with specimen curation.

References

- Castro, L.R. & Dowton, M. (2006) Molecular analyses of Apocrita (Insecta: Hymenoptera) suggest that the Chalcidoidea are sister to the diaprioid complex. *Invertebrate Systematics*, 20, 603–614.
- Dowton, M. & Austin, A.D. (2001) Simultaneous analysis of 16S, 28S, COI and morphology in the Hymenoptera: Apocrita – evolutionary transitions among parasitic wasps. *Biological Journal of the Linnean Society*, 74, 1–111.
- Goloboff, P., Farris, S. & Nixon, K. (2003) T.N.T.: Tree analysis using new technology. Program and documentation available from authors and at www.zmuc.dk/public/phylogeny/tnt
- Heraty, J., Ronquist, F., Carpenter, J.M., Hawks, D., Schulmeister, S., Dowling, A.P., Murray, D., Munro, J., Wheeler, W.C., Schiff, N. & Sharkey, M. (2011) Evolution of the hymenopteran megaradiation. *Molecular Phylogenetics and Evolution*, 60, 73–88.
- Johnson, N. F., Masner, L., Musetti, L., van Noort, S., Rajmohana K., Darling, D. C., Guidotti, A. E. & Polaszek, A. (2008) Revision of world species of the genus *Heptascelio* Kieffer (Hymenoptera: Platygastroidea, Platygastriidae). *Zootaxa*, 1776, 1–51.
- Johnson, N. F., Musetti, L. & Janzen, J.-W. (2001) A new fossil species of the Australian endemic genus *Peradenia* Naumann & Masner (Hymenoptera: Proctotrupoidea, Peradeniidae) from Baltic amber. *Insect Systematics & Evolution*, 32, 191–194.
- Musetti, L. & Johnson, N.F. (2000) First documented record of Monomachidae (Hymenoptera: Proctotrupoidea) in New Guinea, and description of two new species. *Proceedings of the Entomological Society of Washington*, 102, 957–963.
- Musetti, L. & Johnson, N.F. (2004) Revision of the New World species of the genus *Monomachus* Klug (Hymenoptera: Proctotrupoidea, Monomachidae). *The Canadian Entomologist*, 136, 501–552.
- Naumann, I.D. (1985) The Australian species of Monomachidae (Hymenoptera: Proctotrupoidea), with a revised diagnosis of the family. *Journal of the Australian Entomological Society*, 24, 261–274.
- Naumann, I.D. (1991) Hymenoptera. (Wasps, bees, ants, sawflies). In: *The insects of Australia. A textbook for students and research workers*. Melbourne University Press, Carlton, pp. 916–1000.
- Naumann, I.D. & Masner, L. (1985) Parasitic wasps of the proctotrupoid complex: a new family from Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). *Australian Journal of Zoology*, 33, 761–783.
- Polaszek, A., Agosti, D., Alonso-Zarazaga, M., Beccaloni, G., de Place Bjørn, P., Bouchet, P., Brothers, D.J., Earl of Cranbrook, Evenhuis, N.L., Godfray, H.C.J., Johnson, N.F., Krell, F.-K., Lipscomb, D., Lyal, C.H.C., Mace, G.M., Mawatari, S., Miller, S.E., Minelli, A., Morris, S., Ng, P.K.L., Patterson, D.J., Pyle, R.L., Robinson, N., Rogo, L., Taverne, J., Thompson, F.C., van Tol, J., Wheeler, Q.D. & Wilson, E.O. (2005) A universal register for animal names. *Nature*, 437, 477.
- Pyle, R.L., Earle, J.L. & Greene, B.D. (2008) Five new species of the damselfish genus *Chromis* (Perciformes: Labroidae: Pomacentridae) from deep coral reefs in the tropical western Pacific. *Zootaxa*, 1671, 3–31.
- Rasnitsyn, A.P. (1980) [The origin and evolution of the Hymenoptera.] *Trudy Paleontologicheskogo Instituta*, 174, 1–192.
- Sharkey, M.J. (2007) Phylogeny and classification of Hymenoptera. *Zootaxa*, 1668, 521–548.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L. & Wheeler, W.C. (2011) Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* doi:10.1111/j.1096-0031.2011.00366.x

- Szépligeti, V. (1903) Neue Evaniiden aus der Sammlung des Ungarischen National-Museums. *Annales Musei Nationalis Hungarici*, 1, 364–395.
- Townes, H.K. (1977) A revision of the Heloridae (Hymenoptera). *Contributions of the American Entomological Institute*, 15(2), 1–12.
- Vilhelmsen, L., Mikó, I. & Krogmann, L. (2011) Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society*, 159, 22–194.

Appendix. Characters used in phylogenetic analysis

1. Length/width A1: (1) ≤ 2 ; (2) ≥ 2.4
2. Length/width A3: (1) ≤ 5 ; (2) > 7
3. Length A1/length A3: (1) < 1 ; (2) > 1
4. Hypostoma: (1) present, visible in posterior view; (2) apparently absent, not visible posteriorly
5. Hypostomal shape: (1) strongly broadened; (2) narrow, nearly lanceolate
6. Malar length/eye height: (1) < 0.6 ; (2) > 0.6
7. Eye height/head width across compound eyes: (1) < 0.7 ; (2) > 0.8
8. Malar length/head length: (1) < 0.4 ; (2) > 0.8
9. Head width across compound eyes/frons width: (1) subequal; (2) > 1.5
10. Head width across compound eyes/head length: (1) < 1.3 ; (2) > 1.3
11. Head width across gena/head length: (1) < 1.3 ; (2) > 1.3
12. Eye height/head length: (1) < 0.6 ; (2) > 0.8 ; (3) $= 0.7$
13. Apex of mandible: (1) distinctly narrowed apically; (2) nearly as wide apically as basally
14. Subbasal ridge on mandible: (1) present; (2) absent
15. Medial notch on distignath of mandible: (1) present; (2) absent
16. Ventral notch on mandible: (1) present; (2) absent
17. Shape of basignath of mandible: (1) fusiform; (2) rectangular
18. Surface of basal portion of distignath of mandible: (1) raised above basignath; (2) not raised
19. Base of distignath of mandible overlapping basignath (best seen in ventral view): (1) yes; (2) no
20. Apex of fore wing: (1) infusate; (2) hyaline
21. Wings of female: (1) macropterous; (2) brachypterous
22. Radial cell of fore wing: (1) closed; (2) open
23. Intersection of m-cu of fore wing: (1) basad of Cu_2 ; (2) intersecting Cu_2
24. Midventral mesepisternal teeth (possibly the trochantins): (1) absent; (2) small, pointed or digitiform
25. Shape of petiole: (1) straight; (2) curved
26. Submedial clypeal projections: (1) present; (2) absent
27. Distance between submedial clypeal projections: (1) none; (2) small (subequal to length of projection); (3) very large (distinctly greater than length of projection)
28. Size/shape of submedial clypeal projections: (1) minute, length subequal to width, rounded; (2) large, broad, pointed; (3) lobate
29. Shape of apical margin of clypeus: (1) convex to straight; (2) concave
30. Shape of female metasomal segments beyond petiole: (1) laterally compressed; (2) cylindrical or weakly depressed
31. Length of T2/length of T3: (1) much > 1 ; (2) ≈ 1
32. Extent of occipital carina: (1) reaching oral margin; (2) abbreviated, broadly separated from hypostomal carina
33. Ventral margin of mandible near posterior articulation: (1) convex; (2) sinuate
34. Lower margin of mandible: (1) convex; (2) concave
35. Position of notauli in relation to transscutal articulation: (1) close or touching; (2) distinctly separated
36. Lateral face of pronotum: (1) nearly glabrous; (2) distinctly setose
37. Sculpture of lateral face of pronotum: (1) smooth; (2) punctate; (3) striate
38. Sculpture of axillae: (1) smooth; (2) punctate
39. Form of line of separation of axillae from mesoscutellum: (1) pits; (2) continuous sulcus
40. Sculpture of lateral lobe of mesoscutellum: (1) smooth; (2) crenulate; (3) mixed; (4) striate
41. Position of mesoscutellar pit in relation to transscutal articulation: (1) reaching; (2) separated
42. Sculpture of mesoscutellar pit: (1) crenulate/striate; (2) smooth

43. Shape of mesoscutellum: (1) length subequal to width; (2) length distinctly > width
 44. Anterior edge of mesoscutellum: (1) straight or weakly sinuate; (2) evenly, distinctly curved
 45. Shape of metascutellum: (1) quadrate, as long as wide; (2) weakly transverse, slightly wider than long; (3) distinctly transverse, strongly wider than long
 46. Shape of anterior metanotal pit above metascutellum: (1) linear; (2) crescentic; (3) rectangular
 47. Size of ovipositor: (1) elongate, extending at least through apical half of metasoma; (2) minute, confined to apex of metasoma
 48. Overall shape of female metasoma: (1) straight, not elongate; (2) elongate, falcate

Ropronia	11211111221112221122112112??1121111222?411212311
Maaminga	2122?21122111222111212?1113122211111312112223111
Dissoxylabis	212111112212122221?212?112??12111122212112221111
Ismarus	2111111?1213112221?2112112??121111?2 [1 3] 11111111111
atratus	222121112221222221221121212211222111311321222322
satyrus	222222112121222211 [1 2] 11121213321222211121321223222
megacephalus	2222211121112222112111212132212222211 [1 2] 1211123122
eurycephalus	222121112111222212221121212211221121311411212122
serratus	222121112221222212211121212111221121112121123222
aurifer	222122221112211121121121212111222112221421223222
segmentator	22212111222121211221112121221122111111222223122
klugi	2222211121112122111111212132212222111212122?2222
variegatus	222121112111212121121121212111222121111421123122
velatus	222122221112212221221121212111222111111311123122
cultratus	222222221112222212221121212111221121112411123322
paulus	2221 [1 2] 1112221222222221221112111221111312411112122
pallescent	22222111211121221121112121211221111111411123122
porteri	222121112221222121221121112111222121112311212322
exul	222122221112222211221111112111222111112421223122
comptus	22211222111212221222112212??13121111112421222322
cracens	22211222111212221222112322??13121111112412123122
australicus	22211111222112221222111312??13111112221321223222
hesperius	22211111222112221222111212??13111112221121223222
antipodalis	22211211211111221222111212??13121112221321223222
peruvianus	21111222111212221222221312??12111121111211211322
chilensis	21111211222112221222221312??12111111311411221322
intonsus	22212111222122222122112121211122211111211111122
bicolor	2221211122232222122111212132212221111113??2?1122
mocsaryi	222122221112222211211121213321222211321212123122
glaberrimus	2222?2221112211211211121211211222121112??1?3122
cubiceps	22212 [1 2] [1 2] [1 2] [1 2] [1 2] [1 2] [1 2] 2 [1 2] [1 2] 2 [1 2] 1 [1 2] 2112121211122212111 [1 2] [2 4] 2 [1 2] 2 [1 2] [2 3] [1 3] 22
fuscator	222121112 [1 2] [1 2] 1212121 [1 2] 2112121211122 [1 2] 1 [1 2] 1 [1 2] 1 [1 2] [2 3] 4 [1 2] [1 2] [1 2] [1 2] [2 3] [1 2] 22